

The importance of Icelandic riverplains as breeding habitats for Whimbrels *Numenius phaeopus*

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90 ECTS thesis submitted in partial fulfillment of a
Magister Scientiarum degree in biology

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General Introduction

Threats facing waders

Nearly half of the wader (Charadrii) populations with known trends are declining, the main cause being loss and degradation of habitats (International Wader Study Group 2003), especially due to intensification of agriculture and wetland drainage (Sutherland et al. In press). Wetland habitats are being lost at an alarming rate (Bildstein et al. 1991; Brown et al. 2001; MacKinnon et al. 2012), the situation being especially serious for species using the intertidal zone of the East Asia-Australasian Flyway where rapid coastal land reclamation is likely the key driver for population declines of up to 8% per year for some species (MacKinnon et al. 2012).

The migration patterns of waders make them particularly vulnerable to habitat changes. They often rely on relatively few staging sites where they congregate in high numbers. Because many waders undertake long migrations (Handel & Dau 1988; Gudmundsson et al. 1991; Gill et al. 2009), conservation of critical sites must be coordinated over vast distances, often involving several different countries (Brown et al. 2001). High site fidelity of many species (Evans & Pienkowski 1984) adds further to their susceptibility to habitat loss (Bildstein et al. 1991). Few studies have been able to address the demographic consequences of habitat loss but one example comes from Redshanks (*Tringa totanus*) that lost their winter habitat and were forced to move to another location. It was shown that the relocated birds suffered from weight loss and increased mortality rate (Burton et al. 2006).

Climate change is also expected to affect waders in various ways. One consequence is rising sea levels that could claim up to 22% of the world's coastal wetlands by 2080 (Nicholls et al. 1999). Another is the fact that the tree line has been moving further north and forest has invaded wader breeding habitat in the arctic tundra (Soja et al. 2007). There is evidence that some wader species are responding to climate change. In Britain, wintering waders have been moving closer to their breeding grounds (Rehfishch et al. 2004) and arrival dates for several wader species have been moving forward in Iceland although only the ones that are wintering relatively close to their breeding grounds seem to be able to respond to the changing conditions (Gunnarsson & Tómasson 2010).

The genus *Numenius*

Forty percent of all waders belong to the Scolopacidae family. The major groups include curlews (*Numenius*), godwits (*Limosa*), phalaropes (*Phalaropus*), *Tringa* and *Calidris* sandpipers, and snipes (*Gallinago*). Vast majority of the family is migratory (Burger 1984). Status of species of the curlew (*Numenius*) genus is generally rather poor (Wetlands International 2006) but these birds seem to be vulnerable to threats like hunting and habitat

change (Berg 1992; Brown et al. 2001; Gregory et al. 2004; Delany et al. 2009). Their slow reproduction, large size and selectivity in habitat use may play a role (Owens and Bennet 2000; Brown et al. 2001).

The Slender-billed Curlew (*Numenius tenuirostris*), that is believed to breed in Russia appears to be on the verge of extinction (Wetlands International 2006), one of the main causes being excessive hunting in the past (Delany et al. 2009). The Eskimo Curlew (*Numenius borealis*) which formerly bred in Canada is believed to be extinct but there have been no confirmed sightings since 1939 (Wetlands International 2006). The main reason for the population collapse is believed to have been intensive hunting (Brown et al. 2001). Eurasian Curlew (*Numenius arquata*) is found at temperate latitudes in the Palearctic, from Ireland in the west to China in the east (Delany et al. 2009). The species is in decline (Wetlands International 2006) which is linked to agricultural intensification (Berg 1992; Gregory et al. 2004). Populations of the Long-billed Curlew of North America are also declining (Wetlands International 2006). Threats to breeding populations include agricultural conversion of native grasslands (Pampush and Anthony 1993) and encroachment of woody vegetation due to fire suppression (Samson and Knopf 1994). The status of the small population of Bristle-thighed Curlew that breeds in western Alaska is thought to be stable (Wetlands International 2006).

The Whimbrel (*Numenius phaeopus*)

The Whimbrel (*Numenius phaeopus*) breeds both in the Nearctic and Palearctic regions in boreal, subarctic and arctic zones (Skeel & Mallory 1996). Whimbrels are generally split into five distinct subspecies, four of which breed in Eurasia (Engelmoer & Roselaar 1998).

N.p.phaeopus breeds in Scandinavia, the Baltic States and northwestern part of Russia. Some decline has been reported in Scandinavia but the European population seems to be relatively stable. Trends in the Russian population are unknown (Delany et al. 2009). Majority of *N.p.islandicus* breeds in Iceland with smaller populations in the Faeroes, the UK and presumably in Greenland. The large Icelandic population is believed to be stable (Delany et al. 2009) but after an increase in the mid-eighties, the population in Shetland has suffered a major decrease (A. Perkins, pers. communication). Some decrease has been reported in the Faeroes as well (Delany et al. 2009). *N.p.alboaxillaris* is believed to breed south and south-east of the Urals in Russia as well as in adjacent parts of Kazakhstan (Delany et al. 2009). It was thought to be extinct when few pairs were found east of the Ural mountains nesting on meadows and fields adjacent to floodplain meadows. Low numbers of this subspecies are believed to be a consequence of a long-term habitat alteration in the region of steppes to farmland as well as climate change with increasing dryness in the area (Morozov 2000). Population trends in *N.p.variegatus*, which breeds in north-eastern Siberia, are unknown ((Wetlands International 2006).

N.p.hudsonicus breeds in Alaska and Canada (Delany et al. 2009). It is now sometimes considered a separate species, the Hudsonian Whimbrel *N. hudsonicus*, that is made up of two subspecies *hudsonicus* and *rufiventris* (Engelmoer and Roselaar 1998). *N. hudsonicus rufiventris* is found from Alaska east to the Yukon. The population of *N.h.rufiventris* is considered to be stable (Wetlands International 2006) while the population of *N.h.hudsonicus* breeding by Hudson Bay seems to be declining (Wetlands International 2006; Watts & Truitt 2011). Causes of this decline are unknown but alteration of vegetation in breeding habitats due to climate change could be a contributing factor (Tape et al. 2006; Ballantyne & Nol 2011).

Tomkovich (2008) concluded that Whimbrels in Central Siberia differ significantly from the West Siberian *N. p. phaeopus* and from East Siberian *N. p. variegatus* and suggested they get the status of a separate subspecies, *N. p. rogachevae*.

Whimbrels from breeding populations in Eurasia winter mostly in Africa, *N. phaeopus* along the western and southern coast as well as on the western Indian Ocean. *N.p.islandicus* main wintering areas are along the western coast of Africa while *N. p. alboaxillaris* is believed to winter along the eastern coast. Wintering areas of *N. p. variegatus* range from South Asia to Australasia and *N. hudsonicus* winters along the coasts of southern North America, South and Central America, and the Caribbean (Delany et al. 2009).

Whimbrels nest in various open habitats, such as dwarf-shrub heaths, alpine heaths, wet moorlands and sandy areas with stunted vegetation (Cramp & Simmons 1983). They are site faithful and return to the same territory year after year (Grant 1991; Gunnarsson 2000) although, like most birds (Greenwood 1980), the females seem less likely to do so than the males (Skeel 1983; Grant 1991; Gunnarsson 2000). Whimbrels are monogamous and the pair-bond seems to be sustained whenever both birds return to the breeding area (Skeel 1983; Gunnarsson 2000). They are territorial and shortly after arrival to the breeding area, males establish territories which the pair then defends together (Skeel & Mallory 1996). Nests are shallow bowls that are scraped out or pressed down in the ground, often lined with some vegetation such as leaves, grass, sedge or small twigs (Skeel & Mallory 1996). Whimbrels in Manitoba frequently use hummocks or mounds for nest sites but also nest in grass and on gravel (Skeel 1983). In Iceland, whimbrels commonly nest within Arctic rush (*Juncus arcticus*) and willows (*Salix* spp.) as well as on hummocks (Gunnarsson 2000).

Clutch size is usually 4 eggs (Skeel & Mallory 1996), both sexes incubate and tend to the brood after hatching. The female sometimes abandons the family before fledging (Cramp and Simmons 1983) while the male stays with the chicks for some time after they have fledged (Grant 1991). The female's part in the incubation might be higher than the male's (Skeel 1976).

Nest success varies across time and range. Near Churchill, Manitoba, nest success has ranged from 14-86% (Jehl 1971; Skeel 1983; Ballantyne & Nol 2011). In Alaska, hatching success for Whimbrels was 66% (McCaffery 1996) and in Finland, 64% of nests survived (Pulliainen & Saari 1993) while 72% of eggs hatched in Shetland (Grant 1991). In Iceland, 61-100% of nests hatched in a riverplain habitat over a three year study but only 1-19% on a heathland area. (Gunnarsson 2000).

Fledging success varies widely as well. In Alaska, no more than three of 24 nests fledged young (McCaffery 1996). Mean fledging success in Shetland was 0.85 fledged chicks per pair. Whimbrels nesting in a riverplain habitat in Iceland fledged on average 1.7 chicks per pair while the proportion was 0.33 chicks per pair in a heathland area (Gunnarsson 2000).

Predators of eggs and chicks are variable between parts of the range but include gulls (*Larus* spp.), jaegers (*Stercorarius* spp.), Common Raven (*Corvus corax*), Northern Harrier (*Circus cyaneus*), Golden Eagle (*Aquila chrysaetos*), Rough-legged Hawk (*Buteo lagopus*), Gyr Falcon (*Falco rusticolus*), Short-eared Owl (*Asio flammeus*), weasels (*Mustela* spp.), arctic fox (*Vulpes lagopus*) and red fox (*Vulpes vulpes*) (Skeel & Mallory 1996).

Departure of adults from the breeding grounds begins in late June and peaks in Northern Europe in mid- to late July. The juveniles follow from late July to early September (Delany et al. 2009). In Iceland, the first Whimbrels have already departed from their breeding territories in late May – early June (Gunnarsson 2010). Migration across Europe and Africa occurs both along the coast and overland. When migrating in autumn, large concentrations at staging sites have not been observed and some Icelandic birds are suspected to make long overwater flights directly to Africa (Cramp & Simmons 1983).

In their winter quarters, Whimbrels are found in a wide variety of coastal habitats, such as intertidal mudflats, mangroves, salt marshes and coral reefs (Cramp & Simmons 1983). Whimbrels tend to defend feeding territories on the wintering grounds (Mallory 1982; Zwarts 1990; McNeil & Rompré 1995) and are site-faithful to their wintering territory (Zwarts 1990) although this varies between areas as Whimbrels in South Africa feeding on mudprawns were not territorial (Turpie & Hockey 1993). Territoriality in waders on the wintering grounds can vary within species and individuals and is thought to be a reaction to limited food resources (Recher & Recher 1969). On the wintering grounds, crabs, especially fiddler crabs (*Uca* spp.), are the main food item along with other marine invertebrates while on the breeding grounds whimbrels eat land invertebrates and berries (Skeel & Mallory 1996).

Spring migration from Africa begins in March (Delany et al. 2009) and passage through Europe reaches its peak in late April (Zwarts 1990) where the birds gather in high numbers in relatively few staging sites in Western and Central Europe (Delany et al. 2009). The passage of Whimbrels in South Ireland, which are presumably mostly of Icelandic origin, peaks in late April (Pearce & Wilson 1980).

An estimated 40% of the world population of Whimbrels breeds in Iceland where they show a clear preference for sparsely vegetated riverplains (Gunnarsson et al. 2006). Regular floods in these areas keep the vegetation structure at a primary stage (Nilson & Dynesius 1994) and suitable for open-habitat species like the Whimbrel. River regulation (Verkefnisstjórn um gerð rammaaætlunar um nytingu vatnsafls og jarðvarma 2011), along with disappearance of glaciers due to climate change (Overpeck et al. 1997) and spread of alien plant species (mainly *Lupinus nootkatensis*) (Magnusson et al. 2001) are likely to cause dramatic changes in these areas in coming decades, resulting in taller and denser vegetation, which could negatively affect the Whimbrels breeding there.

The results of a three year comparison of a riverplain area and a heathland area in 1997-2000 showed that breeding success was much greater in the riverplain, possibly due to higher food supply and less predation (Gunnarsson 2000) but studies at a larger spatial scale are needed to validate this pattern.

Study objective

The aim of this study was to compare the breeding success of Whimbrels between the favoured habitat (riverplains) and other Whimbrel habitats to achieve an estimate of the relative importance of the threatened riverplain habitats for breeding Whimbrels in Iceland and worldwide. I firstly (a) compared two specific sites (one riverplain and one grassland) to obtain detailed information about the fate of nests and chicks of individually marked adults, nest predators and food availability, and secondly (b) surveyed three additional riverplain sites and three sites in other habitats to attain larger-scale measures of breeding density and breeding success. The results are presented in manuscript I. In manuscript II, generalized linear models were used to determine the utility of biometric data to sex Whimbrels.

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The importance of Icelandic riverplains as breeding habitats for Whimbrels *Numenius phaeopus*

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Abstract

Capsule Threatened riverplain habitats in Iceland, which hold a substantial proportion of the world population of Whimbrels, had much higher breeding densities than other habitats but proportion of successful breeders was similar between habitats.

Aim To estimate the conservation value of preferred breeding habitats of Whimbrels through comparison with other breeding habitats at different spatial scales.

Results Whimbrels breed consistently at much higher densities in the preferred riverplain habitats than in other habitats frequently used by the species in Iceland. Breeding output measured as the proportion of breeding pairs with chicks did however not differ significantly. Comparison of resource abundance between riverplain and other habitats was not conclusive, possibly due to two volcanic eruptions which may have affected invertebrate abundance in the study areas. We estimate that c. 22% of the Icelandic population of Whimbrels and c. 10% of the world population of the species breed in riverplains in Iceland.

Conclusion The study shows that the threatened riverplain habitat in Iceland is an important breeding ground for Whimbrels but further work is needed to elucidate the drivers of habitat preferences.

Keywords: Breeding density, breeding success, habitat selection, Whimbrel, Iceland.

Introduction

Habitat specialisation is one of the factors that contributes to species vulnerability to habitat loss (Owens and Bennet 2000). Species which show preference for specific habitats are by definition disproportionately distributed between different habitats, therefore factors affecting the preferred habitats are selective towards the species in question. The variation in demographic parameters between preferred habitats and other habitats will however determine the effects of habitat change on populations as habitat preference does not necessarily translate into similar variation in demographic rates. Such effects can operate through density dependence, such as reduction in average fecundity through increased competition in preferred habitats (López-Sepulcre et al. 2010) which can buffer population changes when preferred habitat is altered. Estimating the variation in demographic rates between habitats that differ in apparent suitability (assessed by preference of individuals towards different habitats) is therefore key in estimating the effects of habitat change on population demography.

Many of the world's wader species (Charadrii) are currently in decline due to loss and degradation of habitats, especially due to intensification of agriculture and wetland drainage (Sutherland et al. In press). Currently, 48% of wader populations with known trends are declining (International Wader Study Group 2003) and Iceland hosts internationally important numbers of several species, e.g.: Golden Plover (*Pluvialis apricaria*) (52%), Purple Sandpiper (*Calidris maritima*) (46%), Whimbrel (*Numenius phaeopus*) (40%) and Ringed Plover (*Charadrius hiaticula*) (32%) (Gunnarsson et al. 2006). Approximately 250 thousand Whimbrel pairs breed in Iceland, representing the bulk of the subspecies *N.p. islandicus* which also has much smaller populations in Greenland, the Faeroes and the UK (Gudmundsson 2002; Wetlands International 2006). The status of the large Icelandic population is believed to be stable (Delany et al. 2009) but the population in Shetland has suffered a major decrease (Perkins, A. pers. communication) and some decrease has been reported in the Faeroes as well (Delany et al. 2009). Icelandic Whimbrels show strong habitat preference for sparsely vegetated riverplains. Although they occur in several other habitats, mostly heathland, wetland and grassland at lower densities, they do not show clear preference for these habitats (Gunnarsson et al. 2006). The results of a three year comparison of a riverplain area and a heathland area in 1997-2000 showed that breeding success was much greater in the riverplain, possibly due to higher food supply and less predation (Gunnarsson 2000) but studies at larger spatial scales are needed to validate this pattern.

These riverplain habitats comprise a rather small portion of Iceland's lowland or an ca. 8% (Gunnarsson et al. 2006). They are most extensive along large glacial rivers but occur also along smaller rivers. Regular floods interrupt vegetation succession in these areas, keeping the vegetation structure at a primary stage (Nilson and Dynesius 1994) and suitable for open-habitat species like the Whimbrel. Damming of rivers for hydroelectric powerplants

may disrupt seasonal flood regime and can alter the plant and animal composition in riverplains (Nilsson and Dynesius 1994; Merritt and Cooper 2000). River regulation (Verkefnisstjórn um gerð rammaaætlunar um nýtingu vatnsafls og jarðvarma 2011), along with disappearance of glaciers due to climate change (Overpeck et al. 1997) and spread of alien plant species (mainly *Lupinus nootkatensis*) (Magnusson et al. 2001), are likely to cause dramatic changes in these areas in coming decades, resulting in taller and denser vegetation. These changes are likely to affect breeding Whimbrels in these areas. Tall vegetation seems to negatively affect breeding success in the closely related species Long-billed Curlew (*Numenius americanus*) (Redmond 1986; Gregory et al. 2011) and Whimbrels in Canada avoid habitats with encroaching woody vegetation (Ballantyne and Nol 2011).

Here we compare the breeding output of Whimbrels between the favoured habitat (riverplains) and other habitats. We firstly (a) compare two specific sites (one riverplain and one grassland) regarding the fate of nests and chicks of individually marked adults to access detailed breeding success, and secondly (b) survey three additional riverplain sites and three sites in other habitats to attain larger-scale measures of breeding density and breeding success. This gives an estimate of the relative importance of the threatened riverplain habitats for breeding Whimbrels.

Methods

Study sites

The study took place in the summers of 2009-2011 in Southern Iceland, which is the largest lowland area in the country. The study was conducted on two levels. A detailed comparison was made between two sites (henceforward referred to as main sites). The main riverplain site in Fljotshlid (63°43,150'N, 20°0,274'W) covered 0,9 km² and characteristic plant species included Arctic rush (*Juncus arcticus*), Woolly willow (*Salix lanata*) and Tea-leaved Willow (*Salix phylicifolia*). The area was grazed by sheep and horses. The comparative site was a mosaic of grassland and heathland area, bisected by the river Eystri Ranga and covering in total 1.4 km². On the western side (63°48,346'N, 20°9,576'W) the area was divided into a rather dry, sparsely vegetated part that ascended up to a more vegetated ledge and was grazed by sheep. The area on the eastern side (63°47,529'N, 20°8,990'W) was grazed by horses.

In addition to the main sites there were six additional survey sites, three riverplain areas and three heathland/grassland areas, where whimbrel pairs were counted regularly over the breeding season to obtain a large scale comparison of breeding density and breeding output between riverplain habitats and other breeding habitats of Whimbrels (see Table 1 and below).

Bird marking on main sites

Birds were caught on nests using a tilting cage (RB60, <http://www.moudry.cz/>), individually marked with a combination of colour rings and weighed to the nearest 5 g with a Pesola balance. Exposed culmen and total head were measured to the nearest 0.1 mm with vernier calipers, flattened wing chord and tarsus-toe length to the nearest 1 mm with a stopped ruler; in addition 8-10 breast feathers were plucked to obtain DNA for sexing. Chicks at different age were marked when caught, weighed, and total head and tarsus-toe measured.

Breeding density and breeding success

Density of breeding pairs in the two main study sites was estimated by mapping nests and territorial birds, many of which were individually marked. In the remaining areas, breeding density was estimated by mapping birds that showed alarm behaviour. If there were two birds together that were not seen being aggressive towards each other, they were assumed to be a pair. Single territorial birds were also assigned the status of a pair and assumed that the mate was absent or incubating. In 2010 and 2011, counts were performed every two weeks, beginning the 1st of June when peak arrival time has finished (Gunnarsson 2010). Counts were usually conducted on the same time of day, in the afternoon and early evenings, due to diurnal differences in detectability (Davidsdottir, 2010). The estimated

proportion of birds that managed to hatch one or more chicks was obtained by comparing the number of birds that were still present in late July, when the vast majority of nests should have hatched and the oldest chicks are about to fledge, with the number of birds in the same areas during the nesting period. This method has been used successfully for at least two related species to obtain estimates of large-scale breeding success (Grant et al. 2000, Gunnarsson et al. 2005). In 2009, counts for all sites were only attained for the fledging period, during July, but comparison on incubation and chick rearing was obtained for all sites in 2010 and 2011.

Nests were located in the main sites by watching birds that showed territorial behaviour from inside of a car until they returned to their nests, or when birds were flushed up of their nests at close range. Eggs were floated and expected hatching date and onset of incubation was estimated according to an incubation plan (based on Liebezeit et al. 2007). Nests in which incubation started on the 15th of June or later were excluded as these are likely to be second attempts (this date was chosen with respect to confirmed relays by marked birds). Nests were usually visited twice a week to determine nest success or failure. In cases where nests were predated early during incubation, clutches were considered complete if the nest had contained four eggs or, if fewer, if the eggs had reached a minimum of 40° angle from the bottom when placed in a water container. Successful hatching of clutches was confirmed by finding chicks in or close to the nest, with remains indicative of hatching (small parts of eggshell, shell membrane) in the nest lining or by alarm behaviour of adults nearby. In 2010, motion-triggered cameras (Scoutguard SG560V in camouflage, HCO) were placed by nests to monitor predation. The cameras were attached to poles and positioned facing north about two meters from the nests and as low as possible (around 10 cm from the ground) to avoid detection from predators. The cameras were programmed to take 3 pictures when triggered with a seven second interval and sense level was set to high.

Chicks of marked pairs in the main sites were counted within a week of fledging in 2010 but Whimbrel chicks fledge when they are 28-30 days old (Grant 1991). Marked pairs were monitored and watched from a distance, usually on more than one occasion, to estimate minimum brood-size. Two pairs from the riverplain area were omitted from analysis. One which might have relaid but the second clutch could not be located and one where only the female had been colour ringed and shortly after hatching she disappeared, leaving the fate of the brood unknown. Mature chicks of unmarked birds on the main study sites were also included in calculations of final brood sizes for these adults. The movement of marked birds suggested that they stayed largely within their territories so it is unlikely that the inclusion of broods of unmarked birds biased the data.

Food availability on main sites

To estimate variation in habitat quality, food availability on the main study sites was estimated by setting 10 pitfall traps in each area in 2010 and 2011. The traps were 9 cm in diameter and were placed in two rows across the study areas, 200 m apart. Captured invertebrates ≥ 3 mm in length were assumed to be possible food items and were identified to major groups (mostly orders but for the beetles, families were possible to discriminate) and counted.

Statistical analysis

Daily survival probability (DSP) of nests was calculated according to Mayfield (1961, 1975) and standard error of DSP was calculated according to Johnson (1979). Comparisons of DSP were made using the method given by Hensler and Nichols (1981). Data was transformed when assumptions of normality where not met or non-parametric tests used.

Calculations were done using the statistical software R (version 2.13.1, R Development Core Team).

Results

Breeding density and breeding success

Density of nesting pairs was on average higher in riverplain areas than in other habitats in both 2010 and 2011 (Figure 1) with breeding density being significantly higher in the riverplain areas in both years (2010; $t = 5.385$; $df = 4$; $p = 0.005$ and 2011; $t = 2.978$; $df = 4$; $p = 0.038$). Despite the average breeding density in the riverplain areas being lower in 2011 than in the previous year, the difference was not significant ($t = 2.236$; $df = 4$; $p = 0.084$) nor was this same comparison for the other habitats ($t = 0.200$; $df = 6$; $p = 0.848$).

Average density of pairs with chicks was also significantly higher in the riverplain habitats than in other habitats in both 2009 (Wilcoxon's rank-sum test; $W = 16$; $p = 0.028$) and 2010 ($t = 6.786$; $df = 6$; $p = 0.0005$), but not in 2011 ($t = 1.732$; $df = 5$; $p = 0.147$) (Figure 1). However, in 2011, the density of pairs with chicks was significantly lower in both habitats than it was in 2009 (riverplains: $t = -7.467$; $df = 6$; $p = 0.0003$; other habitats: Wilcoxon's rank-sum test; $W = 0$, $p\text{-value} = 0.026$) and in 2010 for riverplain sites ($t = -6.040$; $df = 6$; $p = 0.001$) but not for other habitats (Wilcoxon's rank-sum test; $W = 1.5$; $p = 0.074$). Density of pairs with chicks was higher in 2009 than in 2010 and this difference was significant for riverplain habitats ($t = 2.701$; $df = 6$; $p = 0.036$) but not for other habitats (Wilcoxon's rank-sum test; $W = 12.5$, $p = 0.243$). (Figure 1).

There was no relationship between breeding density and large scale breeding success in 2010 (linear regression: $y = 0.864 - 0.008x$; $R^2 = 0.155$; $p = 0.181$) or in 2011 (linear regression: $y = 0.531 - 0.011x$; $R^2 = 0.168$; $p = 0.172$). On average, the proportion of pairs in riverplain areas that were still present during chick rearing in 2010 was 59%. In other habitats, this proportion was 67% ($\chi^2 = 0.087$; $df = 1$; $p = 0.768$). In 2011, this proportion was 28% on the riverplain sites and 40% in other habitats ($\chi^2 = 0.128$; $df = 1$; $p = 0.721$).

Hatching success on main sites

Incubation started on average on the 29th of May ($SE = 1.00$) on the main study sites. The earliest date of incubation was 20th of May (three nests at the riverplain site and three at the grassland site). There was no difference in the onset of incubation between the main study sites in either year (2009: $t = -0.55$; $df = 24$; $p = 0.587$, 2010: $t = -1.30$; $df = 14$; $p = 0.215$) nor was there difference between years for each area (Riverplain: $t = 1.34$; $df = 17$; $p = 0.199$, grassland: $t = 0.61$; $df = 21$; $p = 0.551$). In 2011, too few nests were found to allow comparison.

Estimated hatching success on the riverplain site in 2009 was 19% with daily survival probability (DSP) of 0.945 and 29% with DSP of 0.958 in 2010 (Table 2). On the grassland site, estimated hatching success in 2009 was 17% and DSP 0.941, whereas in 2010 the hatching success was 15% with DSP of 0.936. There was no difference in daily survival of

nests between the riverplain and grassland site in 2009 or 2010 and neither was there a significant difference between years within each habitat (Table 2).

The most common cause of nest and egg losses was predation but between 58 and 65 % of eggs were predated on both main sites in 2009 and 2010 (Table 3). Other causes of egg loss were abandonment (3%) and 1% of eggs were infertile. In 2010, cameras were placed by and monitored a total of 15 nests (8 on the riverplain site and 7 on the grassland site) for a varied length of time (range 1-20 days, mean=8.6 days). The cameras recorded 13 predation/destruction events (Table 4). On one occasion the nest robber was an Arctic fox (*Alopex lagopus*) and that was the only time the nest was emptied completely in one round, leaving no remains. On three occasions Arctic skuas (*Stercorarius parasiticus*) removed one egg at a time (from two nests). Horses ruined one nest in two rounds and sheep were responsible for the rest of the events (7). Only sheep and horses were caught on camera taking eggs on the riverplain site, all other events took place on the grassland site. In addition to the camera recordings, Raven (*Corvus corax*) was seen robbing one nest on the grassland site and eggs with clear markings from a bird beak (probably an Arctic skua) were found outside another predated nest.

Fledging success on main sites

In 2010, 11 pairs on the riverplain site produced a total of 19 chicks of which 21% (4) fledged. This gives 0.36 fledged chicks on average per pair (Table 5). On the grassland site, 14 pairs produced 22 chicks and 7 (32%) of them were assumed to have fledged (0.5 fledged chicks/pair). There was not a significant difference in proportion of chicks that fledged between the main study areas ($\chi^2 = 0.178$; df = 1; p=0.67).

Average broodsize on the riverplain site was 1.3 chicks per pair (n=7). On the grassland site, average broodsize was 1.5 chicks per pair (n=6). Difference in brood sizes between the habitats was not significant (Wilcoxon rank sum test. W = 16.5, p = 0.5). No chicks were confirmed to have fledged in 2011.

Adult return rate and duration of territory attendance

In total, 28 adults were ringed in 2009, 14 females and 14 males. Ten birds were marked on the riverplain site in 2009 and 70% of them were resighted the following year. On the grassland site, seven of nine marked birds returned in 2010 (78%). Seven females (50%) and 10 males (71%) were resighted in 2010 but the difference was not significant ($\chi^2 = 0.60$, df = 1, p = 0.439). In 2010, 26 additional birds were ringed, 13 males and 13 females, 12 from the riverplain site and 14 from the grassland site. Of 23 ringed males present in 2010, 17 returned in 2011 (74%) while 10 of 20 females were resighted (50%) but the difference was not significant ($\chi^2 = 1.70$; df=1; p=0.193). Twelve birds of 19 present in 2010 were resighted in 2011 on the riverplain site (63%) and 57% returned to the grassland site (12 of 21 birds).

In 2009, birds were last seen in the main study areas in the second week of August but in 2010, the vast majority of birds, both marked and unmarked, had left the main study sites by the end of July. Of marked birds in 2009, 31% remained in the areas in August (8) but only one of 43 (2%) in 2010. There was a significant difference in proportion of marked birds that still remained in the areas in August between years (Fisher's exact test; $p=0.001$).

Food availability

Overall, total food availability was similar between the main study sites in 2010 (Numbers of invertebrates; riverplain: 2.00 ± 0.28 /trap day; grassland: 2.21 ± 0.25 /trap day; Wilcoxon's rank-sum test; $W = 46$; $p = 0.796$) but there was significant difference for three groups. More individuals of family Curculionidae were trapped on the grassland site (Wilcoxon's rank-sum test; $W=2$; $p = 0.00023$) as well as Hymenoptera ($t = -2.364$; $df = 13$; $p = 0.035$) and Gastropoda (Wilcoxon's rank-sum test; $W = 23$; $p = 0.045$). Other beetles (mainly beetles of families Elateridae, Staphylinidae and Byrrhidae) were more common on the riverplain site but this difference was not significant (Wilcoxon's rank-sum test; $W = 76$, $p = 0.054$).

In 2011, the total food availability on the riverplain site was lower than the previous year although the difference was not significant ($t = 1.959$; $df = 14$; $p = 0.07$). However, this difference was significant for Carabidae beetles ($t = 4.943$; $df = 9$; $p = 0.0008$), other beetles ($t = 2.886$; $df = 12$; $p = 0.014$), Diptera ($t = 5.473$; $df = 10$; $p = 0.0003$) and Hymenoptera (Wilcoxon's rank-sum test; $W = 67$; $p = 0.015$)(Figure 2). There was significantly lower total food availability on the grassland site in 2011 than in 2010 ($t = 2.567$; $df = 12$; $p = 0.025$) and that difference was mostly in the numbers of Diptera ($t = 4.771$; $df = 9$; $p = 0.001$). There was not a significant difference in overall food availability between the riverplain and grassland site in 2011 ($t = -1.256$; $df = 8$; $p = 0.243$) but there was significant difference in numbers of Curculionidae (Wilcoxon's rank-sum test; $W = 0.5$; $p = 0.007$) and Lumbricidae ($t = -2.767$; $df = 4$; $p = 0.047$), with more on the grassland site.

Discussion

Differences in Whimbrel breeding habitats in South Iceland

The breeding densities of Whimbrels in riverplain areas in southern part of Iceland are among the highest recorded worldwide. In this study, the average breeding density at the riverplain sites over two years was 29 ± 2.3 pairs/km² whereas a previous study found stable breeding densities over a period of 3 years around 40-45 pairs/km² in the same habitats (Gunnarsson 2000). The highest density in a heathland area in Shetland was 21.4 pairs/km² (Grant 1991) and in Churchill, Manitoba, 11.5 pairs/km² were recorded in a hummock-bog habitat for the subspecies *Numenius phaeopus hudsonicus* (Skeel 1983). Despite this high breeding density, we found no apparent relationship between breeding density and hatching success which was similar for riverplain areas and other habitats. This is contrary to Gunnarsson's study (2000) where hatching success and subsequent fledging success were much greater in the densely populated riverplain area than in the heathland area. The study areas surveyed by Gunnarsson (2000) study seem to represent extremes when it comes to hatching success, an estimated 61-100% of nests hatched each year on the riverplain but only 1-19% on the heathland site. In Canada, hatching success was also highest in the most densely populated habitat (Skeel 1983). Estimated hatching success in the main riverplain site in this study was 19-29% while the nest success in the grassland site was 15-17%. Hatching success among waders is known to vary greatly among species, in time and between areas (Evans and Pienkowski 1984) and documented hatching success for Whimbrels ranges from 14-86% (Jehl 1971; Skeel 1983; Grant 1991; Pulliainen & Saari 1993; McCaffery 1996; Ballantyne & Nol 2011).

Chick survival from hatching was rather poor when compared to an earlier study (Gunnarsson 2000), with 21% at the riverplain site and 32% at the grassland site. In Gunnarsson's study, the difference in breeding success was mainly due to much higher hatching success in the riverplain area. Chick survival from hatching was also slightly higher in the riverplain site with average survival from hatching to fledging 52% while it was 38% at the heavily predated heathland site, but this difference was not significant.

Motion detecting nest cameras caught 13 egg predation/destruction events and in most cases sheep were responsible (they were seen with their snouts in the nestcup in the photos). Egg and chick eating by sheep is a known phenomenon (Palsdottir 1992; Furness 1988), thought to stem from mineral deficiency (Furness 1988). Mammalian predators seem to be the main robbers of wader nests (see review by MacDonald and Bolton 2008) and arctic foxes were suspected to have predated several nests in the current study and an earlier study (Gunnarsson 2000). However, sheep participation in egg predation should not be underestimated and may have had considerable local impact at the main study sites.

There was no difference in minimum survival rate (return rate) of marked birds between the main study sites. The return rates reported here are similar to the results from

Gunnarsson's study (2000) where annual return rates were 60-82%, with no significant difference between his study sites despite the marked difference in hatching success. In Canada, whimbrels seemed to show more site tenacity towards the habitat with higher hatching success (Skeel 1983). The numbers for return rates in Iceland are somewhat lower than those found for whimbrels in Shetland (Grant 1991) where return rates were 87% for males and 68% for females. In 2011, many birds were only seen once and therefore some birds might have gone undetected. The spring and early summer of 2011 was unusually cold and another eruption started in Grimsvotn, S-Iceland, adding ash to the amount already present from the previous year. Very few pairs seemed to even attempt breeding at the main study sites that year which may have lowered the detection rate. In the current study as well as in Gunnarsson's (2000), females seemed less likely to return although the difference between the sexes was not significant. This might be due to insufficient sample size since such difference was found in Shetland (Grant 1991).

Consequences of selecting distinct breeding habitats

The Ideal free distribution theory (Fretwell and Lucas 1970; Fretwell 1972) predicts that for habitats of differing quality, the best areas will have the highest density of breeders but as more individuals move in, the value of the habitat declines until reaching a point where it is equally profitable to move into the second best habitat. High breeding density in riverplains might therefore simply be a response to food supply there being higher than in other habitats (assuming the results from an earlier study (Gunnarsson 2000) provide a more accurate estimate of food availability in riverplain areas than the results presented here, see below). Density of many bird species has been shown to be positively correlated with food availability (e.g. Holmes 1970; Cody & Cody 1972; Newton et al. 1977; Miller & Watson 1978; Seastedt & MacLean 1979; Enoksson & Nilsson 1983) although it is uncertain whether birds adjust their territory size to available resources or if they are unable to fend off competitors for the preferred habitats. The assumptions of the IDF theory are that individuals are able to select the habitat that maximises their fitness, also individuals are able to enter any habitat and that all individuals are equal. Although the IDF provides a useful null-model to predict distribution and fitness, the assumptions are rarely met. For birds, like most waders, which show strong adult philopatry (Evans and Pienkowski 1984) and natal philopatry to a certain degree (Thompson & Hale 1989; Jackson 1994; Gunnarsson et al. 2012) the assumptions of flexibility in site selection are violated and spatial knowledge of site quality is probably limited, especially for waders that breed in subarctic and arctic areas and have therefore very limited time to complete their breeding cycle (Meltote et al. 2008).

Grant (1991) compared Whimbrel productivity between five sites in Shetland 1986-1988. There was no difference in hatching success between the sites but fledging success differed. However, variation in productivity could not be directly linked with variation in nesting densities and the two sites which had the highest fledging success per pair were the

ones with highest and lowest nesting densities. The results presented here and Grant's (1991) indicate that the relationship between breeding density and breeding success among whimbrels might not be straightforward. Higher nest density might lead to higher predation pressure (e.g. Krebs 1971; Göransson et al. 1975; Schmidt & Whelan 1999). Predation on Snowy Plover (*Charadrius alexandrinus*) nests in California seemed to be density dependent (Page et al. 1983). But high density could also be beneficial when it comes to defending against aerial predators. Whimbrels are very adept flyers and aggressively mob much larger birds (Jonsson & Gunnarsson 2010) and higher density means more birds joining chases with less effort per individual bird (Gunnarsson 2000). In an experimental study with artificial nests, predation was significantly lower where the aggressive lapwings (*Vanellus vanellus*) and Curlews (*Numenius arquata*) were present and defended against aerial predators (Göransson et al. 1975).

It is also possible that high density in riverplains has led to such severe competition that differences in breeding success between habitats has disappeared, as has been shown with Seychelles magpie robins (López-Sepulcre et al. 2010). Gunnarsson (2000) noted that brawls between neighbouring Whimbrel pairs were common in the riverplain area, especially during chick rearing. In this study, conflicts after territories had been established did not seem to be frequent.

The strength of natal philopatry is unknown in Whimbrels. Of 71 chicks banded in Manitoba, two (both males) were recovered three years later nesting in their natal habitat, both within 2 km from their hatching sites (Skeel 1983). In the closely related Long-billed Curlew (*Numenius americanus*), male chicks that were resighted did not attempt to breed until their third year but one female paired up as a two year old (Redmond & Jenni 1982). Natal philopatry among Long-billed Curlews is significantly male biased (Redmond & Jenni 1982) as well as for Black-tailed Godwits (*Limosa limosa islandica*) in Iceland (Gunnarsson et al. 2012).

Assuming that Whimbrels, especially males, return and attempt to breed in their natal area suggests that the high density in riverplain areas in S-Iceland was achieved through breeding success being on average higher in these habitats, possibly due to higher food abundance (Gunnarsson 2000) and, as the density increases, joint defence of the breeding habitat (Gunnarsson 2000; Jonsson & Gunnarsson 2010). Based on the results presented here, if such difference in breeding success between riverplains and other habitats in S-Iceland exists, it is likely to be a consequence of chick survival rather than hatching success, contrary to Gunnarsson's results (2000).

Whimbrels are long lived and the evolution of habitat selection probably only requires slight differences in productivity or survival over long time periods. It can therefore not be excluded that Whimbrels on riverplains have a higher fitness on average that went undetected in this study.

Influence of volcanic eruptions on food abundance

One of the main drivers of difference in productivity is food abundance (Gardarsson & Einarsson 1994) but no difference was detected between habitats in this respect in the current study. The invertebrate sampling is likely to have suffered by two volcanic eruptions in 2010 and 2011. Volcanic ash is known to have adverse effect on many invertebrate groups although the effect varies between taxons and life stages (Akre et al. 1981, Brown and bin Hussain 1981, Johansen et al. 1981, Shanks & Chase 1981; Marske et al. 2007). Remains of Curculionidae were found in all chick fecal samples (n=13) gathered in 2009 and often in high numbers. The supply of these beetles on the riverplain site in this study was much lower than on the riverplain site by River Thjorsa in an earlier study (Gunnarsson 2000), along with fewer Carabidae beetles as well. Dipteran flies also seemed more common by River Thjorsa but the difference was not significant, probably due to small sample size of seven traps by River Thjorsa and high variance. The abundance of other groups were similar between the sites although slightly higher by River Thjorsa.

It is probable that ash deposit in the main sites in 2010 and 2011 negatively affected food availability and may have done so disproportionately between habitats as the riverplain site was closer to the eruptions. This in turn could have negatively affected chick survival.

Whimbrel breeding habitats in South Iceland: implications for conservation

Riverplain areas in South Iceland sustain a large number of Whimbrels (this study; Gunnarsson 2000, Gunnarsson et al. 2006). Many of these areas are likely to undergo rapid changes in vegetation in coming years due to disappearance of glaciers, river control and encroachment of introduced species such as *Lupinus nootkatensis* and the native willows (*Salix spp.*) which spread when grazing declines (Schulz & Leininger 1990). Regular floods in these plains keep the vegetation height and composition suitable for open-habitat species like the Whimbrel and taller vegetation will likely make these areas uninhabitable for the species. Whimbrels in Canada avoid encroaching woody vegetation and in Idaho, Long-billed curlews (*Numenius americanus*) flew 5-10 km away from their territories to feed in a spring of unusually tall vegetation in their territories that appeared to hinder their foraging. This was associated with delayed nesting, reduced clutch size and smaller eggs that year (Redmond 1986; Redmond and Jenni 1986).

Almost half of the estimated world population of Whimbrels breeds in Iceland and evidence suggests that riverplains are under threat so estimating the relative importance of this key habitat for population demographics is important for successful conservation. Riverplains in Iceland constitute around 8% of Iceland's lowlands (c. 1902 km²; Gunnarsson 2006). In this study we found that the breeding density on riverplains was on average 29 pairs/km². The Icelandic population is thought to consist of 250 thousand pairs (Gudmundsson 2002) and from that we can roughly estimate that c. 22% of the Icelandic population breeds in riverplain areas, which means that c. 10% of the world population

breeds in this habitat in Iceland. However, further studies are needed to estimate demographic parameters and resource abundance in these habitats with more accuracy.

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Figures

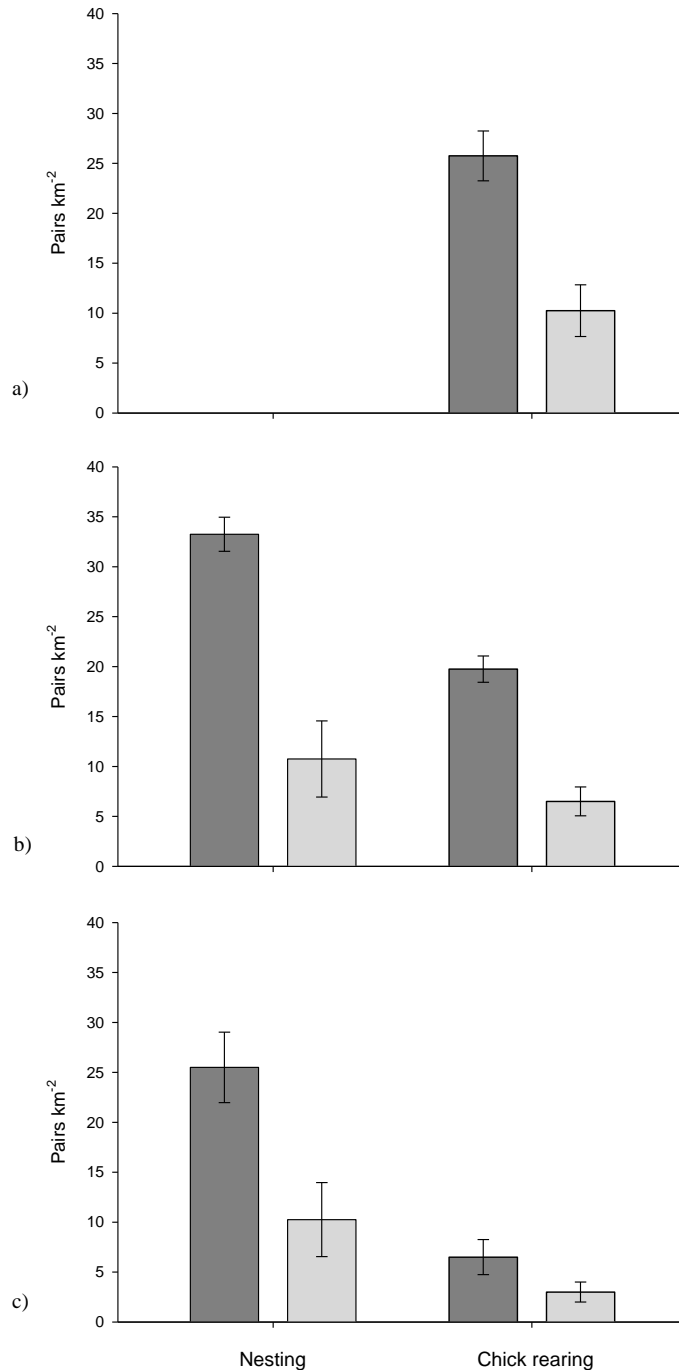


Figure 1. Comparison of density of breeding Whimbrels between riverplain habitats and other habitats a) during chick rearing in 2009, b) during nesting and chick rearing in 2010 and c) during nesting and chick rearing 2011. Density of nesting pairs on riverplain sites was 33.3 ± 1.7 (SE) pairs/km² in 2010 and 24.5 ± 3.5 pairs/km² in 2011 whereas in other habitats it was 10.8 ± 3.8 pairs/km² in 2010 and 9.8 ± 3.2 pairs/km² in 2011. Density of pairs with chicks on riverplain sites was 25.8 ± 1.9 pairs/km² in 2009, 19.8 ± 1.3 pairs/km² in 2010 and 6.5 ± 1.8 pairs/km² in 2011 whereas in other habitats it was 10.0 ± 2.4 pairs/km² in 2009, 6.5 ± 1.4 pairs/km² in 2010 and 3.0 ± 1.0 pairs/km² in 2011. Riverplain areas are shown with dark grey bars and other habitats with light grey bars.

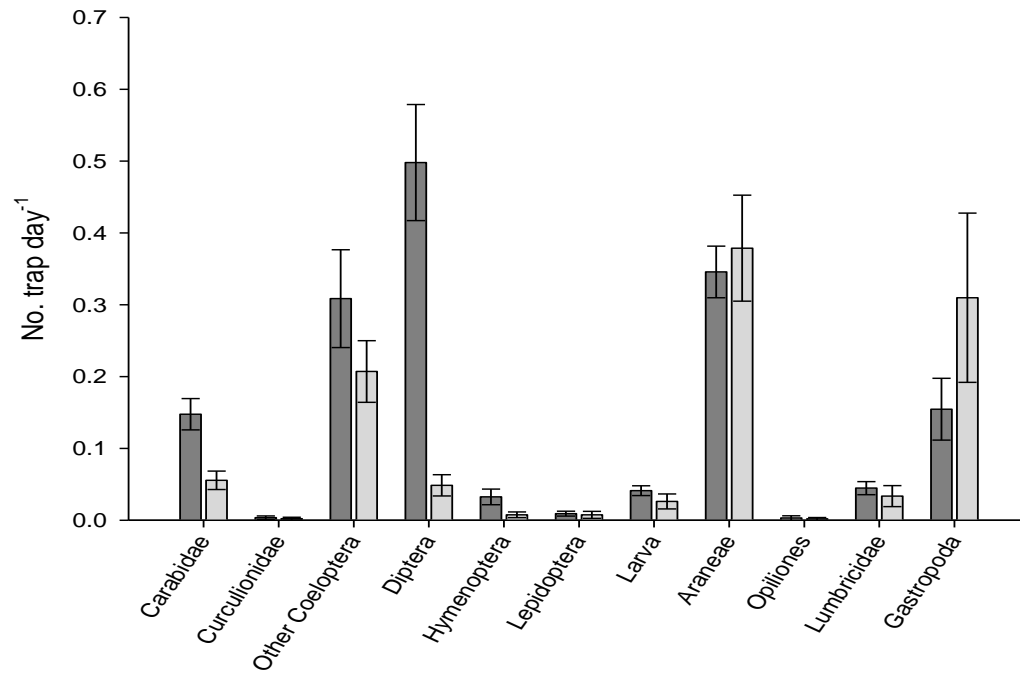


Figure 2. Comparison of average numbers of invertebrates caught in pitfall traps in the riverplain area in 2010 and 2011. 2010 is shown with dark grey bars and 2011 with light grey bars.

Tables

Table 1. Names, coordinates and area of survey sites.

Habitat	Name	Coordinates	Area (km ²)
Riverplain	Frodholtshjaleiga	63°44.987'N, 20°25.975'W	0.5
	Saudholt	63°50.828'N, 20°39.998'W	0.45
	Arnarbaeli	63°56.629'N, 21°12.659'W	0.6
Other	Hvolsfjall	63°45.671'N, 20°11.915'W	0.6
	Hadegisholt	63°55.924'N, 20°30.699'W	2.5
	Minniborgir	64°4.924'N, 20°43.933'W	1.2

Table 2. *Observed nest success, calculated nest success and daily survival of nests at main study sites.*

Year	Riverplain			Grassland			
	Hatched nests (%) [*]	Hatched nests (%) ^{**}	Daily survival (SE)	Hatched nests (%) [*]	Hatched nests (%) ^{**}	Daily survival (SE)	
2009	33 (n=12)	19	0.945 (0.019)	36 (n=14)	17	0.941 (0.019)	z= 0.179; p= 0.858
2010	47 (n=15)	29	0.958 (0.015)	33 (n=18)	15	0.936 (0.018)	z=0.938; p=0.348
			z=0.516; p=0.606			z=0.175; p=0.861	

* Observed nest success (successful nests/all nests).

** Hatched nests according to the Mayfield method, nesting period of 29 days used in calculations (Grant 1989)

Table 3. *Number of and fate of eggs found at main sites in 2009 and 2010.*

Year	Riverplain					Grassland				
	Eggs	Hatched	Predated	Abandoned	Infertile	Eggs	Hatched	Predated	Abandoned	Infertile
2009	40	12	26	0	2	50	14	32	4	0
2010	59	23	36	0	0	60	22	35	3	0

Table 4. *Identified nest predators recorded on camera in 2010.*

	Arctic fox (<i>Vulpes lagopus</i>)	Arctic skua (<i>Stercorarius parasiticus</i>)	Sheep (<i>Ovis aries</i>)	Horse (<i>Equus caballus</i>)
Riverplain			4	2
Grassland	1	3	3	

Table 5. Fledging success at main study sites in 2010.

Riverplain					Grassland				
No. of pairs	No. of chicks	No. of fledged chicks	Chick survival	Fledged chicks/pair	No. of pairs	No. of chicks	No. of fledged chicks	Chick survival	Fledged chicks/pair
11	19	4	0.21	0.36	14	22	7	0.32	0.50

Table 6. *Return rates of Whimbrels to the main study sites.*

Year	Return rate (%)			
	Riverplain	Grassland	Females	Males
2010	70 (7/10)	78 (7/9)	50 (7/14)	71 (10/14)
2011	63 (12/19)	57 (12/21)	50 (10/20)	74 (17/23)

Sexing of Icelandic Whimbrels *Numenius phaeopus islandicus* using biometrics and DNA

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Abstract

Knowing the sex of individuals is important in many studies of ecology and evolution. Whimbrels (*Numenius phaeopus*) are waders which exhibit no plumage difference between the sexes but some sexual size dimorphism exists, with females on average larger than the males. During the breeding season in Iceland from 2009 to 2010, 50 Whimbrels of the *islandicus* subspecies which breeds in Iceland, the UK, the Faeroes and Greenland, were caught on nests, measured and feather samples taken for DNA sexing. Generalized linear models were used to determine the utility of biometric data to sex the birds. Wing length and body mass were the only components that significantly contributed to the model which correctly predicted the sex of 94% of the birds sexed by DNA, thereof 76% with $\geq 95\%$ certainty.

Keywords: Waders, sex determination, Whimbrel, biometrics, GLM.

Introduction

Reliable sexing of individuals is of high importance in many studies of ecology, evolution and behaviour since the sexes can vary considerably in terms of many life history variables (Durell et al. 1993; Durell 2000; McCloskey & Thompson 2000; Both et al. 2003; Bearhop et al. 2006). Many species of waders show reversed sexual size dimorphism, with the females being larger than the males. This dimorphism is, however, often weak and there can be a considerable overlap in biometrics between the sexes (Prater et al. 1977), making sex determination in the field difficult. Molecular sexing of live birds has made it possible to find biometric methods to determine sex based on measurements for some species (Gunnarsson et al. 2006; Hallgrimsson et al. 2008). The Whimbrel (*Numenius phaeopus*) is a large shorebird of the Scolopacidae family with holarctic distribution that breeds in boreal, subarctic and arctic regions (Skeel & Mallory 1996). It is split into five subspecies, one of which, *N. p. islandicus*, breeds in Iceland, the Faeroes, the UK and presumably in Greenland, and winters mainly in West Africa (Delany et al. 2009). It is on average larger than *N. p. phaeopus* (Engelmoer & Roselaar 1998), subspecies which is found in Scandinavia, the Baltic States and northwestern part of Russia during the breeding season (Delany et al. 2009). Whimbrels show no plumage difference between the sexes although the females are on average larger than the males for all measurements (Prater et al. 1977). Here the reliability of biometric measurements to predict the sex *N. p. islandicus* was tested using generalized linear models (GLMs).

Methods

In total, 50 whimbrels were caught in S-Iceland during the breeding season in 2009 and 2010. Birds were captured on nests using a tilting cage (RB60, <http://www.moudry.cz/>), individually marked and weighed to the nearest 5 g with a Pesola balance. Exposed culmen and head were measured to the nearest 0,1 mm with vernier calipers, flattened wing chord and tarsus-toe length to the nearest 1 mm with a stopped ruler and 8-10 breast feathers plucked for DNA extraction (see Table 1 for measurements). Birds were sexed from DNA obtained from their feathers. The basal part of the calamus was cut and put in 250 µl of Chelex solution (6%) along with 2.5 µl of proteinase K (1%). Two feathers were used for each sample. The sexing method used identifies gender-based variability in the introns of CHD1 genes (Fridolfsson and Ellegren 1999). All PCR reactions were in a volume of 10 µl using 4.48 µl dd H₂O, 0.75 µl dNTP (1mM), 1 µl Tween 20 (1%), 1 µl Taq Buffer (10x), 1 µl BSA (10 mg/ml), 0.34 µl 2550F primers, 0.34 µl 2718R primers og 0.09 µl UAmpliTaq enzyme. 1 µl of DNA extraction was added to the 9 µl PCR solution at first but later the DNA volume was increased to 3 µl and the volume of water decreased to get better PCR reactions. The PCR conditions were as described in Fridolfsson and Ellegren (1999). PCR products were visualized on 1.5% agarose gel with ethidium bromide. Females display one (CHD1W) or two fragments (CHD1W and CHD1Z) while males only display one fragment (CHD1Z) that is clearly different in size from the female-specific CHD1W fragment.

Generalized linear models with binomial errors and a logit link function were used to examine relationships between sex based on DNA, body mass, length of wing, culmen and tarsus-toe, with sex as the binary response variable. Collinearity of the variables was tested with the variance inflation factor (VIF). A VIF value smaller than 10 is generally not of concern (Quinn and Keough 2002). Models predicting sex based on biometrics were compared to sexing results from DNA analysis. One male bird was excluded from part of the analysis because tarsus-toe measurements had to be skipped due to the bird's agitated state while being handled. All statistical analysis was conducted using R (R Development Core Team 2011).

Results

Of 50 birds that were molecularly sexed, 24 turned out to be males and 26 were females. Measures of the birds were all significantly higher for the females (Table 1). Analysis of the collinearity indicated high dependence of the variables when head length was included (VIF for head length = 89.24). By excluding head measures, there was not sign of collinearity between the other variables, with the VIFs for body mass, wing, tarsus-toe and culmen being 1.43, 1.35, 1.77 and 1.73, respectively.

The full model (Eq. 1) correctly sexed 95.9% (47/49) of the birds and 75.5% of those were sexed with $\geq 95\%$ probability of being of the assigned sex (Table 2)(Fig. 1). Omitting culmen from the model (Eq. 2) didn't affect the results (Table 2). Wing length and body mass were the only components that significantly contributed to the model (Eq. 3) and correctly predicted the sex of 46 of 49 birds (93.9%)(Table 2).

(1)

$$P(Female) = \frac{\exp(-195.64547 + 0.21675 \cdot \text{mass} + 0.29630 \cdot \text{tarstoe} + 0.25871 \cdot \text{wing} + 0.01296 \cdot \text{culmen})}{1 + \exp(-195.64547 + 0.21675 \cdot \text{mass} + 0.29630 \cdot \text{tarstoe} + 0.25871 \cdot \text{wing} + 0.01296 \cdot \text{culmen})}$$

(2)

$$P(Female) = \frac{\exp(-196.1569 + 0.2163 \cdot \text{mass} + 0.2600 \cdot \text{wing} + 0.3096 \cdot \text{tarstoe})}{1 + \exp(-196.1569 + 0.2163 \cdot \text{mass} + 0.2600 \cdot \text{wing} + 0.3096 \cdot \text{tarstoe})}$$

(3)

$$P(Female) = \frac{\exp(-157.2132 + 0.1951 \cdot \text{mass} + 0.2752 \cdot \text{wing})}{1 + \exp(-157.2132 + 0.1951 \cdot \text{mass} + 0.2752 \cdot \text{wing})}$$

There was a negative relationship between body mass and mark day, the birds got lighter as the breeding season progressed (linear regression: $y = 514.657 - 1.520x$; $R^2 = 0.154$; $p = 0.003$) although when tested separately for each sex, the relationship was only significant for females (Fig 2). Models with body mass corrected by mark day (with residual mass on mark day) were tested but predictions of those models were poorer than when body mass was used unchanged.

Discussion

The full model based on biometrics correctly predicted the sex of 96% of the birds when compared to the DNA analysis. Wing length and body mass were the components that contributed most to the model and by only including them, the proportion of correctly sexed birds was just slightly lowered from the full model (by one bird out of 49). Body mass of whimbrels is not constant over the breeding season and the birds get lighter as the season progresses. Correcting for time of season did however not improve the model, perhaps because the relationship between body mass and mark day was only significant for female birds. A discriminant function analysis based on length of wing, culmen and tail of study skins of the American subspecies *N.p.hudsonicus* revealed a similar proportion of correctly sexed birds as presented here or 95% (Skeel 1982) although higher proportion of *N. p. hudsonicus* could be sexed correctly with $\geq 95\%$ certainty, or 85%.

Polymorphism in the Z chromosome has been reported for auklets (*Aethia* spp.) (Dawson et al. 2001) and for Black-tailed Godwits (Schroeder et al. 2008), causing some males to display two fragments instead of one which might cause danger of incorrect sexing. In those cases though, other primers were used which amplify a different fragment of an intron on the same gene (Griffiths et al. 1998). When the procedure was repeated with the 2550F and 2718R primers, no such polymorphism was detected (Dawson et al. 2001; Schroeder et al. 2008). The method developed by Fridolfsson and Ellegren (1999) worked well for the whimbrels and results from the agarose electrophoresis were conclusive.

Our results show that wing length and body mass can be used for predicting the sex of Whimbrels *N.p.islandicus* during the breeding season with high certainty. These results are likely to have practical applications for sexing of the *islandicus* subspecies in the countries where they breed and during migration in other European countries.

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Figures

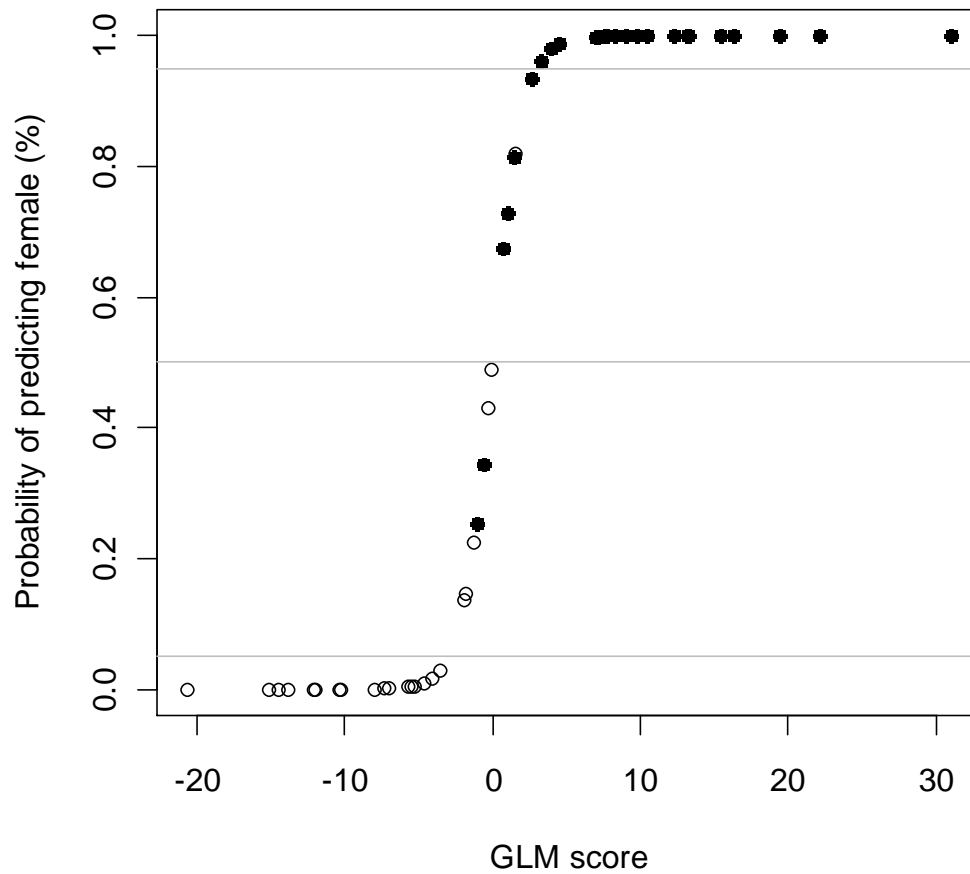


Figure 1. The probability of determining the sex of female Whimbrels using wing length and body mass according to a GLM. Females are shown with solid circles and males with open circles.

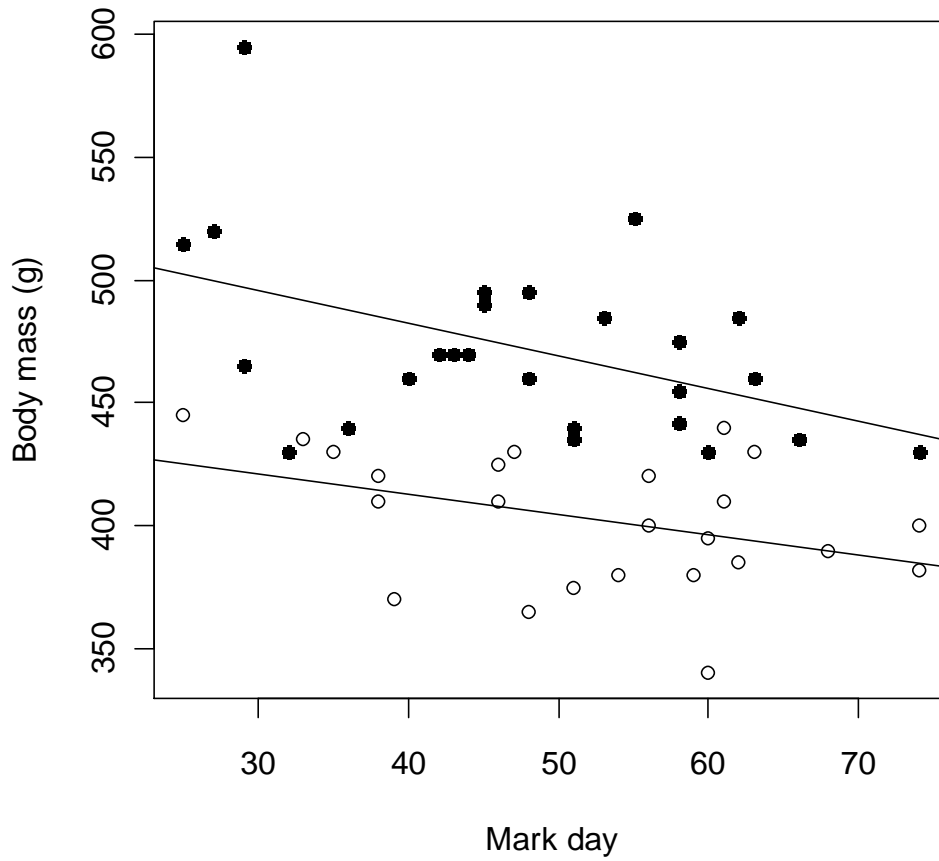


Figure 2. Relationship between body mass of Whimbrels and mark day (as days from 1st of May) and regression lines for the sexes separately (Females: linear regression: $y=535.740-1.334x$; $R^2=0.177$; $p=0.018$. Males: linear regression: $445.668-0.821x$; $R^2=0.116$; $p=0.058$). Females are shown with solid circles and males with open circles.

Tables

Table 1. *Biometrics of N.p.islandicus breeding in S-Iceland.*

	Males (n=24)		Females (n=26)		t	p
	Mean	SE	Mean	SE		
Body mass (g)	402.8	5.5	472.0	7.4	-7.490	<0.001
Wing length (mm)	259.8	1.0	269.8	1.3	-6.128	<0.001
Tarsus-toe length (mm)	107.4	0.6	111.6	0.7	-4.508	<0.001
Culmen length (mm)	82.0	0.8	87.1	0.9	-4.191	<0.001
Head length (mm)	122.8	0.9	129.9	1.0	-5.533	<0.001

Table 2. Comparison of full and reduced models. Deviance and probability are due to the last component added to the models with one degree of freedom. AIC represents the Akaike criterion which reflects the overall fit of the model, with lower values indicating a better fit.

Model	df	Deviance	P	AIC	Correctly sexed (%)	Correctly sexed with ≥95% probability (%)
Sex = wing + mass + tarstoe + culmen	44	0.004	0.949	22.623	95.9	75.5
Sex = wing + mass + tarstoe	45	1.496	0.221	20.627	95.9	75.5
Sex = wing + mass	46	25.329	<0.001	20.123	93.9	75.5
Sex = wing	47	28.292	<0.001	43.453	77.6	28.6